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THE BOTANICAL REVIEW

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THE CYTOLOGICAL ANALYSIS OF SPECIES HYBRIDS. II[1]

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The present article is intended as a supplement to the admirable one on the same subject written by Dr. Karl Sax for the first volume of this journal (126). During the last ten years many papers on hybrid cytology have been written, and our understanding of species relationships in terms of the chromosome behavior of their hybrids has greatly increased. In particular, certain genera, such as *Gossypium, Triticum-Aegilops, Layia, Datura* and *Nicotiana,* have been so intensively studied that hybrids are known involving a majority or practically all of their species. With such knowledge available, cytogeneticists can confidently establish principles concerning the reasons for the chromosomal behavior found in various types of hybrids, and even for the nature of the genetic barriers between species. That age-old problem of biology, what makes species distinct from each other, is gradually being solved by the application of the tool forged for us by the cytologists and geneticists of ten to twenty years ago, and termed by Sax the "permanent hybrid-cytogenetics".

FACTORS INVOLVED IN CHROMOSOME PAIRING

This new knowledge, however, has made necessary very little revision of the general statements made by Sax. His section on "factors involved in chromosome pairing" is as valid today as it was ten years ago. Failure of pairing due to genetic factors, or "asynaptic genes", has been found, in addition to *Zea* and other examples cited by Sax, in *Rumex acetosa* (166), *Pisum sativum* (49), *Nicotiana sylvestris* (45), *Oenothera* (17), *Gossypium hirsutum* × *barbadense* (10), *Allium amplectens* (75) and *Triticum aestivum* (78). Li, Pao and Li (78) have suggested that the

[1] Supplement to article in The Botanical Review 1: 100–118. 1935.

correct term for this phenomenon is "desynapsis", since in every case where the necessary observations have been made the chromosomes actually are synapsed during early pachytene, and fall apart during late pachytene and diplotene. Genetically controlled abnormalities of spindle behavior have been found in *Zea* (18), *Saccharum* (59), *Lathyrus* (153), in the hybrid *Mentha piperita* × *spicata* (147), and in a *Festuca-Lolium* hybrid derivative (30). In *Lathyrus* the abnormal stretching of the spindle is accompanied by an abnormally great contraction of the chromosomes, a reduction in the number and an increase in terminalization of the chiasmata. In *Secale cereale,* Müntzing and Prakken (95) found occasional sporocytes at meiosis with a larger or smaller number of bivalents than the seven which were to be expected on the basis of the known somatic chromosome number of the plant. This was explained on the basis of an exchange of chromosomal material between archesporial cells in the premeiotic mitoses, or cytomixis. These examples show that genetically controlled abnormalities of meiosis, apart from those produced by lack of structural homology in the chromosomes, are likely to be found occasionally both in good species and in hybrids. Nevertheless, they are rarely if ever the principal cause of cytological irregularities and sterility in species hybrids. In most hybrids between closely related species, the behavior of the spindle and related structures is normal, and the chromosomes are partially or nearly completely paired at prophase and metaphase of meiosis, with subsequent lagging, bridge-fragment configurations and other phenomena now definitely associated with lack of homology. Non-homologous pairing at meiosis has not yet been recognized in any plants besides *Zea,* as reported by Sax (126), so that the presence of pairing and chiasma formation in species hybrids can still be taken as a very probable indication of homology between the parental chromosomes.

FERTILE SPECIES HYBRIDS

The problem of fertile species hybrids must now be considered on the basis of recent definitions of the species, such as those of Clausen, Keck, and Hiesey (20), and of Dobzhansky (34). No less than eleven such definitions, by different authors, are included in the anthology on "The New Systematics", edited by Huxley (57). These authors all agree that isolation barriers of some sort

are essential to build up and maintain the morphological distinctness that enables us to recognize species, and that the sterility of pollen or seed in otherwise vigorous F_1 hybrids is one of the most important of these barriers. All, moreover, are further agreed that two species may under some conditions be effectively isolated from each other even though the F_1 hybrid between them forms perfectly normal pollen and sets a high percentage of seed. Dobzhansky (34, *257*) and Huxley (57, *11*) recognize the importance of physiological isolating mechanisms, such as ecological, seasonal or temporal isolation, wherein the parental forms do not meet. Clausen, Keck, and Hiesey, rejecting these as valid criteria for keeping species distinct, recognize only genetically controlled barriers to gene exchange. They point out, nevertheless, that the sterility of F_1 hybrids is only one of these barriers, and that the weakness or sterility of F_2 segregates, due to their possession of disharmonious combinations of genes from the two parents, must also be considered. They cite as examples of species hybrids which are fertile in F_1, but in which the barrier to gene exchange becomes evident in later generations, *Zauschneria cana* × *septentrionalis* (21), *Layia gaillardioides* × *hieracioides* (22) and *Solidago rugosa* × *sempervirens* (47). Other such examples are *Gossypium arboreum* × *herbaceum* (56, 130, 159) and *Solanum Henryi* × *verrucosum* (114). In addition to these and the genera cited by Sax (126), fertile, cytologically normal F_1 hybrids between species generally recognized by systematists are known in *Antirrhinum* (38), *Aster* (161), *Canna* (101), *Catalpa* (136), *Ceanothus* (81, 82), *Crepis* (7, 16), *Dianthus* (41), the New World diploid species of *Gossypium* (9, 15, 135, 159, 160), *Lycopersicum* (55), *Solanum* (114, 115), *Vaccinium* (31) and *Veronica* (48). In *Antirrhinum, Aster, Crepis, Lycopersicum* and *Vaccinium* evidence either from artificially raised F_2 populations or from hybrid swarms existing in nature indicates that no barrier to gene exchange exists between the parents of the hybrids concerned, once these are brought together. In nature they are kept apart by geographic or ecological isolation. Under the species definitions of Dobzhansky and of Huxley, these entities would be considered distinct species; under that of Clausen, Keck and Hiesey they would not. If one applied the principles of the latter authors to the evidence of Darrow and Camp (31) on *Vaccinium,* one would be forced to conclude that

the entire subgenus *Cyanococcus* consists of but three species, which would be differentiated from each other not on morphological characteristics, but on the basis of chromosome number, the first being diploid, the second tetraploid, and the third hexaploid. This shows that in a number of genera fertile, cytologically normal hybrids between recognized species are the rule, and that to apply to such groups the strictly genetic criteria of species differentiation would make necessary a very drastic revision of present classifications.

SPECIES HYBRIDS WITH SLIGHT IRREGULARITIES OF MEIOSIS

In spite of this difficult situation in the genera mentioned above, the statement of Sax still holds good, that "irregular meiotic divisions and pollen sterility are characteristic features of most species-hybrids". Nevertheless, the great majority of F_1 hybrids produced in the last ten years of which the parents are closely related species show relatively few meiotic irregularities, and at least in a large proportion of their sporocytes the chromosomes are all paired at diakinesis and metaphase. In addition to the four genera cited by Sax, normal or only slightly irregular meiosis in partially or completely sterile hybrids has been found in *Apocynum* (2), *Ceanothus* (81, 82), *Collinsia* (52), *Crepis* (6, 7, 61) *Galeopsis* (90), *Ixeris,* subg. *Crepidiastrum* × subg. *Paraixeris* (102, 103, 104), *Lactuca* (162), *Layia* (22), *Lycopersicum* (73), *Papaver* (39), *Phaseolus* (69, 70) *Populus* (110), *Setaria* (79), *Solanum* (107, 115, 148), *Taraxacum* (112), *Tradescantia* (3), *Tragopogon* (163) and *Verbena* (33). The explanation suggested by Sax (125, 126) for *Campsis,* that the sterility of pollen and egg cells in these hybrids "might be caused by structural hybridity involving only small chromosome segments", has been adopted by Müntzing (93) for both intra- and interspecific hybrids of *Galeopsis,* by Stephens (143) for *Gossypium* hybrids, and by Dobzhansky (34) for *Primula floribunda* × *verticillata.* Upcott (154), after a detailed study of meiosis in the latter hybrid and its allopolyploid derivative, concludes that the sterility of the F_1 is due to unfavorable gene combinations in the gametes. She does not, however, suggest a mechanism by which gene combinations leading to sterility in haploid gametes could when present in a double condition give fertile diploid gametes. Hence the suggestion of Dobzhansky, that the fertility of the allopolyploid *P. kewensis* is due to preferential

pairing between the complete homologues of the doubled parental sets, is still the one most easily understood. Such preferential pairing would not be expected unless the chromosomes derived from *P. floribunda* had slightly different gene arrangements from those of *P. verticillata,* so that their affinity for each other, though strong enough to enable them to pair in the diploid, would nevertheless be weaker than that between the structurally identical chromosomes produced by doubling the somatic complement of the diploid F_1 hybrid.

This increasing number of sterile species hybrids with essentially normal meiosis is of more than usual interest. At least some of them must come from parents only recently differentiated from each other, in which the sterility barrier is as yet incomplete. An understanding of the cause or causes for their sterility should tell us much about how interspecific isolating mechanisms come into being, or more briefly, about the origin of species. This is made even more likely by the discovery that within certain species, such as *Galeopsis Tetrahit* (89, 90, 93), *Oryza sativa* (149) and *Bromus carinatus* (140), there exist strains which when crossed produce F_1 hybrids having sterility phenomena exactly comparable in both kind and degree to those of the interspecific hybrids mentioned above. Müntzing (93), after a careful study of several intra- and interspecific hybrids of this type in *Galeopsis,* favors the hypothesis of hybridity for small structural differences in the chromosomes in all of his examples for two reasons: *a*) in most examples, both intra- and interspecific, he found univalent chromosomes in some sporocytes, which would be most easily explained on the basis of slight reduction in structural homology of the parental chromosomes; and *b*) in a few interracial hybrids of the tetraploid *G. Tetrahit,* but never in the parental strains, he found multivalent configurations in occasional sporocytes, in spite of the fact that the total amount of chromosome pairing was less than that in the parental strains. These could be most easily explained as resulting from interchange of small chromosomal segments between the ancestors of the parental races, or from a reduction of the structural homology of chromosomes derived from the same parental diploid species to such an extent that preferential pairing was partly eliminated. Sturtevant (144) has suggested a mechanism of inversion and reinversion of the same chromosome segment by means

of which metaphase pairing would still appear normal, but would result in gametes with probably lethal duplications and deficiencies whenever crossing-over occurred in the reinverted segment. Similar mechanisms can undoubtedly be hypothesized in regard to translocations. Although, therefore, much more evidence is needed, that which we have favors the hypothesis that the sterility of F_1 hybrids with apparently normal meiosis is in most cases due to the existence of structural hybridity for small chromosomal segments. Partial confirmation of this hypothesis has been obtained by examination of pachytene configurations in *Antirrhinum* hybrids (38), but evidence of this sort is still far too scanty. If the hypothesis is correct, then the data on segregation in F_2 of a hybrid between such closely related species as *Galeopsis Tetrahit* and *G. bifida* (90) indicate that several such small structural differences must exist between two groups of populations before they will become effectively isolated from each other genetically, and thus represent distinct species. Sax (125) suggests that a difference in four or five segmental interchanges would result in almost complete sterility in the F_1. In *Galeopsis,* however, the effect of each structural difference must be less than was conceived by Sax, judging from the nature of segregation in F_2.

STRUCTURAL HYBRIDITY AND ITS EFFECTS

The hypothesis that structural hybridity for small chromosome segments, or cryptic structural hybridity, is responsible for the haplontic sterility (*i.e.,* sterility in the haplophase or gametophyte, *cf.* Müntzing, 90) of hybrids with normal sexual structures and apparently normal meiosis is strengthened by the fact that between hybrids of this type and those which have very irregular meiotic divisions there is a whole series of intermediate types, which show gradually increasing degrees of meiotic irregularity. Hybrids frequently are found in which all of the chromosomes become paired in a large proportion of the sporocytes, but in which many other sporocytes contain unpaired univalents, and there are also such irregularities as lagging chromosomes, chromatid bridges and acentric chromosome fragments. These have been reported in *Aegilops* (63, 64, 127), *Allium* (36, 37, 83), *Crepis* (6), *Godetia* (51, 53), *Gossypium* (1, 9, 131, 134), *Lactuca* (162), *Layia* (22), *Lilium* (118, 119), *Mirabilis* (129) and *Paeonia* (27, 137).

The effect on chromosome behavior at meiosis of structural hybridity for inversions has been most carefully studied in the now classic work of Richardson (119) on *Lilium martagon album* × *L. Hansonii.* Depending on the number and character of the chiasmata or cross-overs within any inverted segment, the configuration seen at first metaphase or anaphase may consist of a single chromatid bridge and a chromatid fragment, of a double chromatid bridge and two chromatid fragments, of a loop and a fragment, or of two loops and two fragments. The two latter configurations, which result from crossing over proximal to as well as within the inverted segment, give chromatid bridges at second anaphase. The interpretation of these configurations is further discussed by Darlington (28, *265–274*). Emsweller and Jones (37) have shown how the segregation of the products of these and other configurations resulting from the pairing of structurally dissimilar chromosomes can produce gametes with new chromosomal types. By far the greater number of such gametes will be deficient for vital sections of chromosome material, but it is possible that viable types of chromosomes may occasionally be formed in this manner. Sveshnikova (145, 146) has reported an instance of this nature in progeny of *Vicia sativa* × *amphicarpha,* but the new chromosome is apparently viable only in the heterozygous condition, and lethal when homozygous. The significance of bridges and fragments as causes of sterility in species hybrids is considerably reduced by the discovery that these configurations, and hence structural hybridity for inversions, are very common in some fertile species, as in *Paeonia* (137) and *Paris* (40).

The presence of rings, chains or other associations of more than two chromosomes, indicating in diploid hybrids structural hybridity for interchanges of relatively large chromosomal segments, has been found in an increasing number of diploid hybrids, both intra- and interspecific (5, 11, 12, 13, 14, 24, 25, 26, 29, 116, 139). The situation in the genus *Oenothera,* in which this type of structural hybridity is most strongly developed, has been ably reviewed by Cleland (24, 25, 26). Here the cytogenetic and morphological picture, although showing certain regularities, is so complex that Cleland is forced to conclude that (26, *27*) "the North American euoenotheras do not show a clear-cut segregation into readily recognizable species." In *Datura* the number of interchange types is

much smaller, and the balanced lethal mechanism characteristic of *Oenothera* is absent, so that rings of 4, 6, or 8 chromosomes, or plants with 12 bivalents, are most commonly found in interracial or interspecific hybrids (11, 12, 13, 14). Each type of chromosomal arrangement has been designated a "prime type". In *D. stramonium,* ten such types are known, each differing from its closest relative by a single interchange, and giving a ring of four plus ten pairs in hybrids with it. Hybrids between more distantly related prime types may give two rings of four, a ring of six, or more complex configurations. In *D. quercifolia* one of the three types known is the same as one of the prime types (Pt. (2+3)) of *D. stramonium,* and gives twelve pairs in interspecific hybrids (14). However, if other prime types of *D. stramonium* or *D. quercifolia* are used, the *quercifolia-stramonium* hybrids have rings of various sizes, depending on the prime types used as parent. In all other interspecific hybrids of *Datura,* rings of various sizes are found, but no configurations are more complex than those known in certain hybrids between prime types within *D. stramonium* (14). Hence the type of structural hybridity which has led to the formation of prime types is of little or no importance in the differentiation of species in *Datura. Paeonia californica* and *P. Brownii* are intermediate between the *Datura* type of interchange pattern and the *Oenothera* type (139, 158). In both these species of *Paeonia,* forms with the haploid number of five bivalents are known, but other forms may have rings of four, six, eight or ten, or various combinations of rings. The type of ring may be constant in all or nearly all of the plants in a colony, or it may vary greatly from plant to plant. Nevertheless, the geographic distribution of the various types of configurations has a definite pattern, which may reflect in some way the evolutionary history of the species. In *Godetia Whitneyi,* Hiorth (53) reports the presence of a complex series of interchange types in a small section of the range of the species in northwestern California. Elsewhere the segmental arrangement of the chromosomes within the species is so uniform that races from Vancouver Island, the northern limit of the range of the species, give hybrids having seven bivalents when crossed with most other races, including those from the north shore of San Francisco Bay, the southern limit of the species. Since these races with the most widespread segmental arrangement give hy-

brids with seven pairs when crossed with the related *G. amoena,* the interchange types in races of *G. Whitneyi* from northwestern California are believed by Hiorth to be of recent origin. In this area the populations of *G. Whitneyi,* largely isolated from each other by the nature of the terrain, are evolving a complex series of morphological and cytological races, some of which may be incipient species.

Convincing evidence for the phylogenetic alteration of the basic chromosome number by means of large, unequal reciprocal translocations of chromosomal segments has been obtained in *Vicia* (145, 146) and *Crepis* (150). In the latter genus, a model for this process was created by Gerassinova (42), using reciprocal translocations produced by means of x-rays in *C. tectorum.* Then in the F_1 species hybrid *C. neglecta* × *fuliginosa* Tobgy (150) found two types of multivalent configurations, involving different groups of chromosomes. Each chromosome could be identified individually by its size and morphology at both mitosis and meiosis, and was given a letter corresponding to those previously used in phylogenetic studies of the genus. The hybrid has seven chromosomes, A, B, C and D from *C. neglecta* ($n = 4$), and A, B and D from *C. fuliginosa* ($n = 3$). The A and D chromosomes of the two species, although appearing as bivalents or univalents in most of the sporocytes of the F_1 hybrid, formed occasional trivalents, and in 10% of the cells were united to form a single quadrivalent. The remaining three chromosomes, B and C of *neglecta,* and B of *fuliginosa,* found a trivalent in 25% of the hybrid sporocytes, indicating that the B chromosome of *fuliginosa* contains segments homologous to portions of both the B and C of *neglecta.* Morphological and distributional evidence both indicate strongly that *C. neglecta* is more primitive and *C. fuliginosa* is derived from it or a closely related ancestor. Furthermore, the C chromosome of *neglecta,* the one not visibly represented in *C. fuliginosa,* was found to be largely heterochromatic. Hence Tobgy makes the very plausible assumption that during the evolution of *C. fuliginosa* the genetically active material of the C chromosome of its *neglecta*-like ancester became translocated to the B. The remaining inert portion of the C, including the centromere, subsequently became lost. Tobgy concludes that Navashin's (98) "dislocation" hypothesis, involving simple translocations, is a less likely one than that of

Darlington (28, *559*) who postulates unequal reciprocal translocations, or segmental interchange, as a mechanism for alteration of the basic number. Sherman (128) has produced evidence that the four-paired *Crepis Kotschyana* evolved in a similar manner from a five-paired ancestor related to *C. foetida.*

Thus the hypothesis advanced by Darlington on cytological grounds and by Babcock on the basis of comparative morphology, that alterations of the basic chromosome number may involve decrease as well as increase, and are brought about by unequal reciprocal translocation or segmental interchange, has received striking confirmation from studies of the cytology of species hybrids. This mechanism could account for the phylogenetic reduction of the basic number postulated by Avdulov (4) for certain Gramineae, by Manton (84) for some Cruciferae, and by various other authors. Increase of the basic number by a single pair, such as seems to have taken place in *Biscutella* (84), *Fritillaria* (28, *560*) and *Vicia* (145, 146), may also have resulted in part from unequal segmental interchange, as pointed out by Darlington (28). The greater frequency of multivalents in hybrids of *Carex* than in pure species (157) indicates that the extensive aneuploid series of chromosome numbers found in this genus has been formed at least in part by unequal translocations. Wahl (157) made the very plausible suggestion that it is the result of the combined action of polyploidy and reciprocal translocation.

HYBRIDS WITH VERY IRREGULAR MEIOSIS

The type of chromosome behavior usually associated with interspecific hybrids, namely, that involving failure of chromosome pairing, lagging of univalents and other gross chromosomal irregularities, has been found in many diploid hybrids, but is not as characteristic of them as has often been supposed. In fact, during the past ten years hybrids in which the modal number of sporocytes contain two or more univalents have been described in only eleven genera, while hybrids in which the chromosomes are all paired or in multivalent associations at meiosis have been reported in 41 genera. Hybrids with marked chromosomal irregularities have been reported in *Brassica* (151, 152), *Crepis* (6), *Gossypium* (1, 9, 10, 134, 159, 160), *Lactuca* (162), *Layia* (22, 23), *Madia* (23), *Nicotiana* (35, 43, 44, 68) *Oryza* (117), *Paeonia* (137), *Papaver*

(167) and *Triticum-Aegilops* (63, 64, 65, 127). As might be expected, the parents of these hybrids are as a rule more distantly related to each other, according to accepted taxonomic classifications, than are those species which form hybrids with more regular meiosis. In *Crepis, Gossypium* and *Lactuca* all these hybrids with more irregular meiosis are between species belonging to different sections or subgenera, and this is true of most hybrids of this type in *Layia* and *Triticum-Aegilops*. Of the other two genera listed above in which a considerable number of hybrids is known, namely *Paeonia* and *Nicotiana,* the former is clearly a very old genus, with many of its species probably extinct and with most of the diploid species very sharply distinct from each other. In *Nicotiana* there seem to be many hybrids with irregular meiosis whose parents belong to the same species group (43). Apparently the factors which restrict chromosome pairing have evolved relatively rapidly in this genus compared with those which produce the morphological distinctions between species. In general, however, the statement may be safely made that when a species is crossed with its nearest relatives, the interspecific hybrids usually have more or less regular meiosis, with univalents present in a minority of the sporocytes.

The observation of Sax, that in hybrids with irregular meiosis "there is great variability in the amount of pairing in different pollen mother cells", has held true for all the examples described in the past ten years. Furthermore, much of this variation is controlled by environment. In addition, when a cross between two species has been repeated, using different parental stocks, the results have sometimes been very different. The most striking difference is that between the *Allium cepa* × *fistulosum* hybrid obtained by Levan (74, 76), and those obtained earlier by Emsweller and Jones (36) and Maeda (83). In Levan's hybrid, of which the *fistulosum* parent came from a European botanical garden, only 2% of the sporocytes had the full complement of eight bivalents, while this was true in 72% of the sporocytes in the hybrid of Emsweller and Jones. For the latter, the *fistulosum* parent was a Japanese variety. In a later paper (37) these latter authors state in passing, but without giving date, that different hybrids between *A. cepa* and *A. fistulosum,* using still different parental stocks, differ considerably from each other in fertility and chromosome behavior.

POLYPLOID SPECIES HYBRIDS

When polyploidy is involved, chromosome behavior in species hybrids, as Sax (126) pointed out, is complicated by the fact that pairing may occur partly or entirely between chromosomes contributed by the same parent. A striking example of this is *Ambrosia elatior* × *trifida* (62). In this case both species are polyploids, and the 12 chromosomes in the haploid set of *A. trifida* are recognizably larger than the 18 from *A. elatior*. Although a maximum of 10–12 bivalents may be formed, pairing occurs almost entirely between chromosomes of similar size, and therefore contributed by the same parent. Sometimes this type of autosyndetic pairing is found in hybrids between closely related polyploid species, in which allosyndetic pairing between chromosomes derived from the two parents also takes place. This results in the formation of multivalents and of a cytological picture simulating that found in autopolyploids. An extreme example of this is a triploid hybrid between two diploid species, *Lolium loliaceum* × *rigidum* (60). This apparently resulted from fertilization of an unreduced, diploid gamete of *L. rigidum* by a normal haploid gamete of *L. loliaceum*. In some sporocytes of this triploid F_1 hybrid all of the 21 chromosomes were grouped into seven trivalents and the prophase (pachytene) of meiosis resembled that found in auto-triploids. In some hybrids, like those of *Phleum* (91, 99, 100) and *Bromus* (141), autosyndesis occurs between chromosomes which are rarely associated with each other in the parental species. Two explanations of this phenomenon have been offered. Müntzing and Prakken (94) suggest a "special genotypically controlled tendency to bivalent formation"; Darlington (28, *198*), on the other hand, advanced the hypothesis of differential affinity. This is based on the fact that chromosomes pair not as units, but segment by segment. If a nucleus, as in an interspecific hybrid or a haploid, contains chromosomes which have certain larger or smaller segments in common, these segments will pair and form bivalents, in spite of the fact that these same chromosomes contain dissimilar segments that remain unpaired. If, on the other hand, each chromosome in the nucleus has a homologue to which it is similar throughout its length, as well as one with which it has only some segments in common, the chromosomes will show preferential pairing and will be associated predominantly with their exact homologues. Chromosomes,

therefore, show differential affinity in their pairing relationships. They will pair with their exact homologues if such are present, but if these are absent, any two chromosomes that possess in common large or small homologous segments may form bivalents. Skirm (133) obtained good evidence that this occurs in *Tradescantia*. From a single diploid F_1 interspecific hybrid plant he obtained two types of tetraploid progeny, one of which formed quadrivalents with the frequency typical for autopolyploids, and the other of which formed only bivalents. In the first type, which presumably resulted from fusion of an unreduced gamete, no two chromosomes were exactly identical, and therefore, no preferential pairing was found. In the second type, which must have resulted from somatic doubling of the zygote or young embryo, two identical sets of chromosomes were present, and preferential pairing occurred between them. Whether or not this explanation can be extended to cover all examples of failure of multivalent formation in polyploids must await further evidence.

In some polyploid species, different strains exist which have different degrees of autosyndesis within their haploid sets. A particularly good example is that of the wheat-rye hybrids obtained by Lebedev (71, 72). Autosyndesis of *Triticum aestivum* chromosomes in hybrids with *Secale cereale* may vary from a mode of zero to one of five bivalents, with seven possible in some cells. The *Triticum* strains exhibiting these differences were all from Afghanistan, and relatively closely related to each other; in fact two of them were sister seedlings segregating from the same heterozygous parent. There is no evidence that *Triticum* and *Secale* chromosomes ever pair with each other.

The recent literature on allopolyploid and amphidiploid hybrids has already been reviewed by Goodspeed and Bradley (46). In this connection, however, may be mentioned the newer examples in which one or both of the parental genoms of an allopolyploid have been identified by hybridization with the appropriate diploid species. An outstanding example is that of the tetraploid New World species of cotton, *Gossypium purpurascens, G. barbadense, G. hirsutum, G. Darwinii* and their relatives (8, 15, 134, 135, 142, 143, 159, 160), *Brassica carinata, B. juncea* and *B. Napus* (87, 152), *Setaria Faberii* (77), *Godetia nutans* (51, 53), *Bromus carinatus* (140), *B. arizonicus* (141), *Nicotiana Arentsii* (44) *and*

Madia citrigracilis (23). Further new information on the analysis and synthesis of polyploids is found in the excellent review of the more important literature by Clausen, Keck, and Hiesey (23).

In many allopolyploids, such as *Triticum-Aegilops* (63, 64) and certain annual species of *Bromus* (66), the component genoms of related species are partly homologous with each other. In such cases the exact ancestors of the polyploid are hard to identify, and the classification of the genoms into distinct types is difficult or impossible. Hybrids between two such allopolyploids show complex types of chromosome pairing, like those found in *Agropyron junceum* × *repens* (106), the various *Triticum* × *Agropyron* hybrids (105, 109, 111, 113, 123, 155, 156), and the hybrid between sugar cane (*Saccharum* forms) and various species of the genera *Erianthus* and *Sorghum* (58, 88).

THE ORIGIN OF HYBRID STERILITY

Based partly on the evidence from chromosome behavior in diploid species hybrids, many workers (*cf.* 138) now accept a working hypothesis to explain the origin of sterility in F_1 species hybrids. These are believed to originate not through the accumulation of the type of genetic factor responsible for the differences in external morphology and physiology between the groups concerned, *i.e.*, the differences which produce subspecies or races. On the contrary, the separation of species by internal physiological genetic barriers, which are responsible for this sterility, is usually produced by a separate set of genetic factors, which by themselves do not necessarily bring about the visible differences between species. These genetic factors may be separated into two groups. Those of the first group affect the mature F_1 hybrid at the critical stage of the formation of the reproductive organs and the archesporium. They thus produce diplontic sterility (90, *315*), or sterility in the diplophase. Examples are various hybrids of *Paeonia* (124) and *Epilobium* (see 138 for references).

The second and more significant group consists of those types of factors which affect the critical stage of meiosis itself, producing abnormal micro- or megaspores, or cause inviability of the gametophyte or gametes, thereby producing haplontic sterility (90). This group consists of two general types. One type includes genic differences causing upsets of the spindle mechanism, timing rela-

tions and other physiological elements of the meiotic process (17, 18, 30, 59, 67, 75, 78, 147, 153). These produce the genic sterility of Dobzhansky (34). The second and much more widespread type of factors appears to be predominantly if not entirely chromosomal in nature. When the parental species have very different chromosome numbers, as in crosses between diploids and polyploids, or between plants having different degree of polyploidy, the factors for chromosomal hybrid sterility involve largely the irregular distribution of the chromosomes to the poles of the spindle, and the resulting formation of gametes bearing unbalanced chromosome numbers and consequently lethal. If, on the other hand, the parents have the same chromosome numbers and are closely related, the distribution of the chromosomes to the gametes is usually normal or nearly so, and the haplontic sterility is due to inviable conditions within the chromosomes themselves. As explained above, the sterility factors in this case are most likely small structural differences, which are not sufficient to prevent chromosome pairing, but give inviable chromosome combinations through their independent segregation, or inviable new chromosomes through pairing and crossing-over (65, 93, 125, 126, 143). This last type, which can be termed "cryptic structural hybridity", appears to be the most common and significant type of barrier producing genetic isolation between species of higher plants. Although the present evidence suggests that as a rule these different types of sterility factors act independently of each other to a great extent, it is highly probable that some genetic differences between species affect two or more of these different types of sterility.

The existence and partial independence of these different groups of species-isolating factors is indicated by evidence suggesting that they have evolved at different rates in different genera. In *Quercus, Salix, Vaccinium* and other genera in which species with widely different external morphology and physiological adaptations form fertile hybrids, none of these factors has become established. In other genera, *e.g., Galeopsis* (90), *Solanum* sect. *Tuberarium* (115) and *Datura,* many hybrid combinations, even between species that are not very different in external morphology, fail because of incompatibility, and all the hybrids that can be produced have good pairing of the parental chromosomes, and usually at least partial fertility. Here the first group of isolating factors, those affecting

compatibility, appear to have evolved more rapidly than the others. Still other genera, like *Crepis, Layia* and *Gossypium,* have a more or less normal pattern of species differentiation, in which the degree of morphological differentiation, of incompatibility, and of hybrid sterility of the chromosomal type are roughly correlated with each other. In these genera the divergence in morphological characteristics and in the various types of genetic isolating factors appears to have progressed at about the same rate. Then there are genera like *Triticum-Aegilops* in which the majority of species differ strikingly from each other in the external morphology of their chromosomes, and nearly all of the species hybrids, although most of them can be made without great difficulty, are characterized by extreme irregularity in chromosome pairing. In such genera the repatterning of the chromosomes through the accumulation of small structural differences appears to have gone on with exceptional rapidity.

The causes of species divergence with respect to these morphologically neutral genetic isolating factors are not yet clear, but some definite hypotheses concerning them have been formulated. The difficulty of accounting for this divergence through natural selection was already recognized by Darwin (32, ch. 9), and is considered practically insurmountable by most recent authors. There are, however, two evolutionary processes now recognized which are independent of natural selection and which could account at least in part for the divergence. These are the effects of sampling in small populations (drift, random fixation) and hybridization between preëxisting species. The effects of sampling could produce in a small isolated population the random fixation of one or more factors which would not affect intercrossing or F_1 fertility in crosses between members of this population, but would produce such effects in crosses with members of other populations. Earlier in this review evidence has been cited to show the occasional presence of partial incompatibility or sterility in crosses within species. Hence it is not unreasonable to assume that if a large species population should because of a change of environment become segregated into several small geographically isolated ones, some of these segregant populations would develop barriers of genetic isolation separating them from the rest. If, then, such a genetically isolated population should increase again, either through the reversal of the

environmental change or through the appearance in the population of favorable mutations, it would form a species morphologically similar to but genetically distinct from the other populations with which it was formerly united. The differentiation of species in this manner by means of passage through a "bottleneck" or series of "bottlenecks" has been postulated by Wright (165). The second method was suggested by the writer (138). If two species differ by a large number of genetic isolation factors, but nevertheless produce an F_1 hybrid which is partly fertile, new recombinations of these factors should occasionally give in later generations types fully fertile but producing partly sterile hybrids in crosses back to both parents. This result has recently been obtained on a large scale by Lamprecht (69, 70) from the hybrid *Phaseolus vulgaris* × *multiflorus*. In some of these genetically isolated hybrid segregates, greater isolation could result from the occurrence and fixation of additional isolating factors. In the writer's opinion there would be no difficulty in accounting for all genetically isolated plant species as resulting either from passage through a previous bottleneck or from segregation out of partially sterile hybrids between preëxisting species. The species differences in respect to external morphology and physiological adaptation to the environment would in this case be mostly an accentuation of previous subspecies or specific differences. According to this hypothesis, therefore, speciation comes about either through hybridization between preëxisting species or through superposition of genetic isolating factors upon a pattern of intraspecific differentiation into races or subspecies, as postulated by Mayr (85, *160*). Such an hypothesis appears as the natural outcome of our present knowledge of the cytogenetics of species hybrids.

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AUXIN, THE PLANT-GROWTH HORMONE. II[1]

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I. This continuation of the review on auxin in volume 1 of this journal is necessarily incomplete, for more than 500 papers have appeared on the subject in the last ten years, and space does not permit a more extended treatment. Only a few trends in the field will be enumerated, and whenever a number of papers on the subject have appeared in close sequence, usually only one or a few of them are listed, the choice being more or less arbitrary; availability of them in America, and sometimes priority or completeness in their exposition, have been used as criteria for selection. More stress is laid in this supplement on the theoretically important points than on the practical ones, since another review in this journal by Zimmerman on growth hormones has been announced; Zimmerman is one of the chief exponents of less theoretical treatment of the plant hormone field (38). Detailed information can be found elsewhere (8, 9, 31, 49, 56, 74, 84, 89), and the same subdivision will be followed here as in the original review, although the emphasis on subjects has shifted very much.

II. The Avena method is still the principal method of quantitative analysis of auxins. A modification of it (61), the deseeded Avena test, is more sensitive to low concentrations and has been accepted as the standard test in some laboratories. Other qualitative and semiquantitative tests have been described in great number. Only the "green tissue tests" (38) and the pea test (76, 80) need be mentioned. Also, new auxin units have been introduced, W.A.E. of Boysen Jensen (9) and T.D.C. of Avery *et al.* (2), but they have exactly the same disadvantage as the A.E. of Kögl. They all depend on the relative sensitivity of *Avena* coleoptiles to auxin, which sensitivity varies with time of day, season, locality and laboratory. The only more or less absolute unit, although not ideal, is van Overbeek's (53) indoleacetic acid equivalent. It gives the amount of indoleacetic acid inducing the same curvature in the Avena test as the tested sample.

III. Chemical isolation and identification of indoleacetic acid

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from vascular plants has been accomplished (5, 32). This makes it necessary to use the term "auxin" as a generic name for all substances, produced by a plant as growth hormones or as correlation carriers, which give a response in the Avena test.

Concerning the chemistry of auxin *a* and *b*, only a few additional facts have been published (43), showing that inactivation of the auxin *a* and *b* lactons occurs in ultraviolet light. The question whether auxin inside the plant is largely inactivated by visible light is still unsettled (45, 50, 69).

Soon after the discovery of the effectiveness of indoleacetic acid as an auxin (42), a deluge of articles appeared, all publishing the growth-promoting properties of other substances (33, 35, 44, 93). Since these substances vary in activity from highly active to almost inactive, and since they have a fairly wide range of structure, the conclusion was drawn that their effect on plants is an unspecific stimulation (1, 21, 38). Three groups of facts, however, speak against such an explanation of auxin acting as a stimulant.

First, it could be established (41) that all active substances have certain structural characteristics in common: an unsaturated ring with side chain of at least two carbon atoms adjacent to double bond, a carboxyl group in the side chain, and a definite space relationship between carboxyl group and double bond.

Secondly, closer analysis showed that the apparent activity of auxin-like substances is reduced by side-reactions and by secondary properties of those substances which have nothing to do with the growth reaction (6, 72). When only the number of molecules actually partaking in the growth reaction is considered, the molar activity of all auxin-like substances is the same (82, 87).

The third group of facts indicating that the effect of auxin on the growing cell more closely resembles a chemical reaction than an unspecific stimulation will be mentioned under VII.

IV. Production of auxin as a function of the growing condition of the plant has been extensively investigated, and very clear correlations between growth rate of shoots during their grand period of growth and auxin production by the stem tip have been found (3, 89, 94). Nutrient deficiencies, especially of N and Zn, decreased auxin production (4, 63).

Auxin has been found in three forms in the plant (for further discussion see (56, 86)), namely,

Inactive in the Avena test:

a) Bound auxin: extractable with organic solvents; liberated after chymotrypsin treatment (76).

b) Precursor: activated in the plant by enzymatic action in stem tip (55); activated *in vitro* by alkaline hydrolysis (2, 5, 32).

Active in the Avena test:

Free moving auxin; diffuses out of plant into water or agar.

These forms have different functions in the plant. The precursor is the source of all, being transformed into free moving auxin which regulates correlation phenomena, such as photo- and geotropism (85). Part of this free moving auxin becomes bound and then regulates growth.

Many papers have appeared on extraction methods. None is entirely satisfactory or is applicable in all cases. Most troublesome is the phenomenon that many materials, notably leaves, stems and fruits, when extracted with organic solvents, continue to give off auxin for many months (29). Only one conclusion emerges from all this work: in each case the best extraction method has to be found empirically and has to be adjusted to the problem for which data are needed.

Other difficulties may be encountered in analyses of the auxin content of tissues. Inhibitors, for instance, may be present (67) which mask or reduce the actual auxin concentration in the extract (25), or the auxin may be destroyed before or during extraction (52). Dwarf genes have been held responsible for excessive auxin destruction inside the plant.

V. Auxin transport was confirmed as polar inside all living tissues, except when pharmacological doses were applied (90). When, under exceptional conditions, auxin reaches the transpiration stream, it moves with this stream against its normal basipetal direction of transport (36). As soon as this auxin has moved back into living tissues it moves polarly again (62). Polar auxin transport may occur simultaneously with non-polar ion transport (83). Inversion of morphological polarity may be followed by establishment of an inverted polarity of auxin translocation (85).

Much work was done to correlate the polarity of auxin transport with electrical polarity, with little success, however (12).

Protoplasmic streaming was speeded by auxin (18) and was

found to be a function of the concentration of oxygen, sugar, auxin and malic acid applied (71).

VI. In several cases the interrelationships were investigated between auxin and other factors in speeding up stem elongation. Special emphasis was laid on the interaction between auxin and sugar (59) and between auxin and caulocaline (77, 81).

VII. The assumption that auxin is a coenzyme required for some process essential in growth, was greatly strengthened by recent work (14). It was found that about 10% of the normal respiration of *Avena* coleoptile is auxin-controlled, and that this respiration is essential for growth. The auxin might play the rôle of coenzyme in a dicarboxylic acid dehydrogenase in this respiration. This would take auxin completely out of the classification of "stimulant" and make it a specific component of a known chemical reaction. It explains the quantitative relationships between auxin and growth, its specificity and its indispensability.

Further study of the structure of the growing cell wall gave rise to more elaborate theoretical considerations concerning the action of auxin (7, 17, 58).

In addition to the direct and indirect action of auxin on the cell wall, a few other effects of auxin have been invoked to explain their effect on growth. To these belong the effect of auxin on active water uptake by the cell (13, 64), their effect in the so-called preparatory reaction (80) and their effect on the translocation of other growth factors (78).

VIII. The earlier controversies on the effects of auxin on the growth of roots and auxin production by roots have now subsided. Only at extremely low concentrations is root growth accelerated by auxin, but above 10^{-10} molar it is inhibited (24). Very little auxin is synthesized by roots in their tips; most of it must be derived from the top (54, 57).

IX. The number of processes in which auxin is known to take part, besides stem elongation, has greatly increased. It is among these most recently recognized processes that the most practical applications of auxins have developed:

a) Bud inhibition. All investigators agree now with Thimann and Skoog that auxin coming from the growing stem tip is the correlation carrier which prevents development of lateral buds. But there is utter disagreement as to the way in which auxin in-

hibits. The literature on this subject has been summarized (73), and actual auxin analyses of inhibited and non-inhibited buds and adjoining stems have been published (20, 51). Sprouting of dormant buds in potatoes and deciduous trees can be delayed with auxin sprays (30).

b) Initiation of roots on stems is also caused by auxins. This discovery has led to one of the most important practical applications of auxins, the rooting of cuttings with auxins and auxin-like substances. Consequently the number of papers on this auxin effect exceeds that on all other effects, mostly concerning the best method of treatment and the most active compound (extensive lists of plants which can be rooted by auxins are to be found in 48 and 49). A variety of methods of application has been used: at apical end of cutting (15); solutions of about 0.01% at basal end of cutting (37); dipping of base in auxin dispersed in talc (26); dipping in alcoholic solutions of auxins (39). Age of plant from which cutting is taken (74), pretreatment of cutting (16), use of additional root growth stimulators (70, 87) and many other factors influence the rooting response.

Theoretical considerations on the mode of auxin action in the rooting response are found in many articles (*e.g.*, 16, 77, 78).

c) Much work has been done on the anatomical changes in tissues caused by application of auxin; swelling of cells, cell division, dedifferentiation and redifferentiation of cells and tissues are commonly observed (34, 60).

d) Another important application of auxin is based on experiments (22, 27) showing that auxin treatment of unfertilized ovaries or styles of many plants led to the development of parthenocarpic fruits of normal size. It seems that under normal conditions of fruit growth, ovules and young seeds furnish the auxin necessary for growth, which has to be applied externally when no seeds are formed (28). Commercial production of seedless fruits is possible in this way (40).

Application of auxins at a later stage of fruit development may check fruit drop. This is used commercially in some apple varieties to prevent pre-harvest drop (23).

e) Among the cases in which auxin increases cell division, cambial activity is the most outstanding. Application of auxin to stems causes cambial activity over some distance below the point of application (65, 66).

f) Much work has been done on the production and anatomy of abnormal tissues induced by (unphysiologically) high auxin concentrations. In many plants structures closely resembling crown gall can be induced by auxins (11, 46, 47).

g) Many morphological changes of various kinds have been described after application of a variety of substances, some of them resembling auxins in structure (90, 91).

h) Addition of auxin to the nutrient solution may partly overcome zinc and boron deficiencies (19, 63). This effect may be related to the effect of auxin on root activity in general (64).

i) A large number of papers has appeared describing the effects of auxin applied to roots or seeds. Many authors claim that such treatments cause after-effects in the form of increased or decreased growth, earlier flowering, better fruit set, *etc.* But others failed to find after-effects. The described effects are probably of complex origin, and more has to be found concerning the exact conditions under which the growth stimulations are reproducible, before general conclusions can be drawn. It is perhaps suggestive that fertility of soil is correlated with its auxin content (68).

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LIGHT AS AN ECOLOGICAL FACTOR AND ITS MEASUREMENT. II[1]

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INTRODUCTION

Refinement in knowledge and new scientific discoveries follow closely behind the introduction of new scientific instruments and new scientific techniques. And in no phase of botany has this been more evident than in the general field of plants in relation to light. Of outstanding importance has been the general availability of cheap reliable light-measuring devices that use as their sensitive element the photoelectric cell. Equally important have been the advances made in growing plants in controlled environment through the use of newly developed artificial sources of light, particularly the neon and sodium vapor lamps and the filters that transmit definite ranges of wave lengths. As a result recent workers have been able to surpass their predecessors in the accuracy of light measurement and in the precision of light control. And through advances in experimental design and statistical analysis developed by Professor R. A. Fisher and his American disciples (55, 156) they have learned how to analyze the separate and combined effects of varying several factors simultaneously in the same experiment. All three of these developments appeared before 1935 when the original paper under this title was published (148), but had not yet been put to widespread use in botanical research.

Just as the trends in research might have been predicted ten years ago on the basis of new light sources, new light measurement devices and new experimental design and analyses, so today we may predict that advances in understanding the relationship of light to plants during the coming ten years will result from a more widespread use of fluorescent light sources and the introduction of heavy carbon as an indicator element in photosynthesis. We may expect further refinement of the mathematical relationships between total available light and plant growth as a result of the increased general availability of light recorders.

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Considerable confusion has been introduced into the literature by the tendency of many investigators to attribute to light certain responses resulting mainly from other causes. Students of plant life must bear ever uppermost in mind the fact that light, being necessary for the photosynthetic process, cannot be varied widely without introducing the factor of malnutrition or starvation. Plants starved for the products of photosynthesis can no more react normally to other conditions than those starved for nitrogen, for phosphorus or for calcium. Likewise, plants starved for mineral elements or provided an inadequate moisture supply inevitably respond differently to light than do normal plants. With sufficient time for adjustment, plants, like all other living organisms, show wide adaptability to different light conditions. But when adjusted to one they cannot quickly respond to a different light condition. For instance, if adjusted to living under very low light intensity, plants may be injured or even killed by abrupt exposure to a high intensity to which, given ample time, they could have become adapted.

Although in the discussion to follow, the various effects of light on plants will in most cases be considered singly, it must be kept in mind that such effects are by no means independent of other environmental conditions.

In preparing the current review, the writer has omitted several important topics if they were covered adequately in his earlier reviews (47, 148) or in the excellent reviews by other workers (26, 27, 62). Material presented in foreign reviews (146) has been covered in part.

LIGHT MEASUREMENT

Excellent reviews of light measurement technique have appeared in both English and German literature since 1935 (45, 47, 58, 96, 108). These reviews describe the various effects produced by light that are susceptible of measurement and the instruments that have been devised to measure these effects. Tests have been made on shape of absorbing surfaces by Miller (102) and Wallace (173). Flat horizontal surfaces can absorb only the vertical component of solar radiation and hence give lower values than spherical absorbers except when the sun is in the zenith. The ecologist concerned with the light received by a single isolated tree or shrub might

prefer to use the spherical absorber, but those studying the light received by the vegetation of a definite area will find the horizontal absorber satisfactory. The most popular instrument that has come into widespread use since 1935 has been the photoelectric cell in its various forms, particularly the photronic cell with a sensitivity curve approximating that of the human eye (53, 169). Such cells have been built into photographic exposure meters that are highly portable, relatively low in price, and hence available to most ecologists. The exposure meter has a geometric scale, making it particularly useful in measuring light of low intensity. It is not, of course, precise at high intensity.

For many studies, direct reading devices for light measurement need to be supplemented by light recorders and integrators such as used by Wallace (172, 173) and MacLean (91). Sprague and Williams (157) have devised a very ingenious and inexpensive integrating light recorder consisting of a photoelectric cell, condenser, a cold cathode discharge relay tube, a second condenser and a sensitive electrical impulse counter. Sprague reports the cost of these instruments as $12.00 to $25.00 (157, 158). A simple and thoroughly sound instrument for integrating solar radiation over a period of time has been described by Byram and Jemison (31). This consists simply of two pairs of calorimeters, one pair of which receives solar radiation while the other is shielded from it. The radiation is measured directly in gram calories per square centimeter by determining the amount of ice melted by absorbed solar energy.

Certain precautions are necessary to get reliable measurements of light in the forest. With photoelectric cells, care must be taken to avoid over-exposure to intense radiation. Under such conditions the cells solarize, *i.e.*, their sensitivity declines. To avoid this and at the same time to get satisfactory readings of full daylight intensity, flat or spherical opalescent glass screens may be used (172, 173, 183). It is necessary to calibrate each individual screen, and if a plain glass surface is used, it must be exposed at normal incidence to sunlight or allowance made for the reflection from the glass surface with different solar angles. Another way to avoid solarization of photoelectric cells is to use them only to measure the light received from a standard mat surface reflector. The reflector, in so far as possible, should have a perfect diffusing

surface, and as a further precaution the photoelectric cells should be held in such a way as to avoid specular, mirror-like, reflection. Standard high-grade bond paper can be used as such a reflector. When a sheet becomes soiled it should be replaced by a fresh one. Painted boards or white opalescent glass surfaces soon accumulate dirt and even though washed frequently are likely in time to change their reflecting capacity.

A common and important source of error in using direct reading devices, either in the open or in the forest, is to allow light reflected from the clothing of the observer or other objects to reach the sensitive elements (187). Reflected light can be particularly disturbing should the reflector be in a sun fleck and the instrument in complete shade. Smith (155) reported that measurements taken with the photographic exposure meter between 9:00 a.m. and 3:00 p.m., used in conjunction with a board coated with aluminum paint, failed to show up differences resulting from thinning; whereas Walton (176), using technique similar to that described by Smith, found that results of thinning showed up quite satisfactorily. Walton and other observers report much more consistent results when the sky is overcast, thereby avoiding the disturbing influence of sun flecks. But readings made in the forest on cloudy days should be compared with simultaneous readings in the open, as absorption of light by clouds varies widely from moment to moment. Rarely is the sky uniformly overcast for any appreciable length of time. Inasmuch as sun flecks may play a very important role in the life of plants growing beneath forest canopies, sufficient widely distributed measurements should be made in any one habitat so as to sample adequately both complete shade and sun flecks. A still better system was devised by Nägeli (110). He took a great number of readings at various points and at various times of day. Light intensity of the habitat was then expressed in a frequency curve.

Ecologists for the most part have discarded photochemical photometers such as the Wiesner and Clements types. There are, however, situations in which the photographic photometers can be successfully used. Matheson (94) made comparative measurements with a Livingston radio atmometer, solar radiation thermometers, Weston photronic cells and Eder-Hecht photographic photometers. He found the first two both to give unreliable mea-

surements when checked against the Callendar pyrheliometer, whereas the last two, the photronic cell and the photometer, gave satisfactory readings provided their limitations (selective sensitivity to different wave lengths and tendency on the part of the photronic cells to solarize when exposed to high intensity solar radiation) were taken into consideration.

Good progress has been made during the past ten years in building more accurate filters for measuring specific spectral regions (16). Such filters may be obtained commercially from the manufacturers of signal glass and photographic filters, or may be made up by individual workers by tinting cellophane or gelatin with various solutions. The need for precise filters is perhaps much greater in physiological than in ecological studies. Nevertheless, a great many investigators have used such filters in measuring light in the forest and beneath various depths of water in lakes and oceans. In using filters with photoelectric cells, the worker must allow for the selective sensitivity of the photoelectric cell as well as the selective transmission of the filter.

LIGHT CLIMATE

The ecologist studying light conditions in natural habitats today not only has better instruments for measuring light than he had in 1935; he also has at his disposal long-time continuous records of light conditions measured at various stations in North America and Europe. Hand (71) has published tables and isopleths that show the light intensity for each hour of the day and each day of the month at 20 North American stations. Steinhauser (162) and Maurain (96) present similar but less complete information for Europe, giving particular emphasis to the influence of altitude. Byram and Jemison (31) show how the light received at any open station can be approximated by direct computations. Their computations must, of course, be corrected for cloudiness.

Variations in the daily period of illumination with time of year and latitude is one specific aspect of light climate. Though the effect of photoperiod on plants has been treated elsewhere (62), the threshold value of light intensity necessary to produce the photoperiodic response is worthy of note. Several investigators (15, 178, 185) have shown that light of one foot candle, or even slightly less, may be adequate either to induce or inhibit flower formation.

But this occurs only when such light is used to supplement daylight or artificial light of intensities adequate for growth and reserve food accumulation (179). Using one foot candle as a minimum, Greulach (67) has found the length of the photo-periodically effective twilight for north central United States to vary from 11 to 28 minutes with a mean of about 19 minutes. It is significant that one foot candle is only slightly above the intensity of bright moonlight.

Ball (17) found that the red end of the spectrum was far more efficient than the yellow, green or blue in preventing flowering of *Turnera ulmifolia* by illumination at night. This is of rather striking importance, since the low light intensities of early morning and late evening are rich in the red region. The above effect is in direct contrast to ordinary phototropic growth responses, which are stimulated much more by the blue than by the red end of the spectrum.

Several workers (86, 95, 113) have reported that light from street lamps is often of sufficient intensity to cause shade trees growing nearby to retain their leaves in autumn several weeks longer than trees of the same species somewhat more distant from the lamp.

The long arctic summer days are of significance in the growth of plants, both because of the relatively long photosynthetic period each day and because of the photoperiodic response. Both of these influences can, however, be overemphasized. Albright (2), for instance, has pointed out that the tomato, which is adversely affected by a 24-hour day when a portion of that light is supplied from incandescent lamps, thrives quite satisfactorily when exposed to the natural light of 24-hour arctic days. The difference in this case probably is due to the fact that the light of the arctic day, though richer in red than normal daylight, is far lower in infrared than light from an incandescent filament lamp. Arthur and Harvill (9) have shown that the injurious effects of 24-hour illumination to tomato plants can be lessened by decreasing the amount of infrared or by increasing the proportion of either red or blue light in the total artificial light to which the plants are exposed.

Razumov and Smirnova (131) emphasize that the effectiveness of the arctic night light is greatly diminished because of low temperature. Most of the daily photosynthetic activity occurred, he

found, during the day when the sun was relatively high and the temperature warm. On the other hand, Freeland (60) and others have shown that certain conifers, at least, can carry on photosynthesis at a sufficiently rapid rate to more than offset respiration at temperatures of 40° to 50° F., and therefore presumably benefit from light of the arctic night. Printz (130) reports photosynthesis at – 2° C. in *Picea excelsa* and *Pinus silvestris*.

Light intensities in the tropics, though normally higher than in temperate regions, are not, in Veth's (171) opinion, so much responsible for the luxuriant growth as the 12-month growing season. He states that growth increases rapidly up to about 20% to 30% of full tropical sunlight, but decreases slightly as intensities increase above 50%. In tropical regions having a minimum of cloudiness, plants thrive on one-fifth to one-twelfth of full light intensity. At greater intensities respiration due to the higher temperatures more than offsets the benefits from increased light. This is the reason why many tropical plants thrive best in shade.

Various workers have reported that light at high altitudes contains an excess of ultraviolet and for that reason is injurious to plants. In fact, some believe that the upper altitudinal limits of species are determined by their relative tolerance to ultraviolet (39). It may be significant to note here that light, particularly ultraviolet, causes a 30% to 50% increase in respiration rate of plants previously conditioned by holding them in darkness for periods up to 70 hours (64, 65).

Solar ultraviolet intensity and its ratio to daylight fluctuate with the intensity of sun spots (12), but it is not known to what extent such fluctuations in ultraviolet radiation affect green plants or animals. It is known that plants can be easily injured by exposure to ultraviolet of wave lengths shorter than that found in sunlight, but it is less certain whether the high intensity ultraviolet encountered at high altitudes and in the tropics is in itself injurious. Also, it has not been clearly demonstrated that ultraviolet is at all necessary for the development of plants (51, 124, 126, 127).

The modifications in light intensity caused by atmospheric turbidity, vegetative canopies and clear or turbid water are more local in action and hence have been referred to as producing a microlight climate. Turbidity, whether due to haze, smoke or ash in the atmosphere, or silt and clay in water, acts selectively in that it

scatters the short blue rays to a greater extent than the long red and infrared; hence in cloudy weather or within turbid water the light has a higher proportion of red and infrared (33, 72). To a lesser degree a vegetative canopy acts similarly, but the changes in quality caused by scattering or refraction are largely offset by differential transmission and reflection, and by changes in the proportion of direct sunlight to skylight caused by the canopy.

Measurements made beneath forest canopies during the past ten years tend to confirm the conclusion reached in the previous review (148) that changes in light quality resulting from passage through a leafy canopy are of minor ecologic significance (14, 32, 101). This is further borne out by measurements of the light transmitted through leaves and that reflected from them. Compared with herbaceous leaves, those of forest trees have relatively low transmission and relatively low reflection (13). Leaves tend to absorb blue to a greater extent than red, and red more than green. A great deal of blue light from the sky penetrates the canopy, compensating in part for that absorbed by the leaves. Atkins, Poole and Stanbury (14) report that green canopies transmit only 10% more green than blue and 15% more green than red. Sauberer (138, 139) reports measurements of the spectral composition of light that had penetrated one, two, three and four leaves, and of that reflected one to four times from leaves. Foliage that transmitted 3% to 20% of the light through the first leaf allowed only about 1% through the second, and a negligible amount through the third and fourth leaves. Infrared light at 770 mμ reflected four times from leaves was 40%, 16%, 6% and 3%, respectively, and green at 540 mμ 6%, .31%, .0017% and .00095% of incident light. As these measurements indicate, leaves reflect (116) and also transmit (46, 49) relatively large amounts of near infrared, but energy in this region is not directly useful in photosynthesis.

Seybold and Egle (147) evidently believe that leafy canopies do cause changes in light quality of ecological significance. They have made extensive studies of the optical properties of leaves and of leaf pigments. Seybold classifies forest floor species as sun plants—those that appear before the deciduous leaves have unfolded; red-green shade plants—those appearing when the leaves are only partially developed; and green shade plants—those appearing as summer advances. The ratio of chlorophyll A to chloro-

phyll B for the three classes of plants was found to be, respectively, 4.36, 3.01 and 2.60. The ratio of xanthophyll to carotin was 3.6, 5.5 and 5.3 respectively. Corresponding ratios for immersed and submerged water plants were for chlorophyll A to B, respectively, 4.4 and 2.3, and for xanthophyll to carotin, 4.0 and 5.7. The ratios of total chlorophyll to total carotinoids varied only slightly. These changes in the relative concentration of the several photosynthetic pigments are assumed by Seybold to be adaptations to light conditions. The actual significance of this still remains to be demonstrated. Further evidence that minor changes in light quality are of slight ecological significance will be presented later under a description of studies of photosynthesis in natural plant habitats.

Many workers have reported light measurements beneath forest canopies during the past ten years. These show the light beneath the leafless hardwood canopies to be approximately 55%, and to decrease progressively as the leaves unfold until the minimum value, varying from 1% to 5%, is attained (34, 165, 175, 186). Intensities beneath pine canopies have been found by Shirley (152) to vary with age and density of stand. Minimum values for jack pine, 15%, occurred at 30 to 60 years of age. Natural red pine canopies of various ages showed the following intensities: 25–35 years, 7%; 55–65 years, 11%; 90–110 years, 16%; 200 years and over, 44%. Intensities beneath tropical canopies may be reduced to between .2% and 1% of full sunlight (32, 52, 119). Even free standing trees such as occur in apple orchards do not have all their branches or all their leaves exposed to adequate light intensity for maximum photosynthesis (35). Schmidt (141) measured light intensities of 24% to 36% beneath apple trees. Likewise, light intensity available to plants growing near buildings or along the border of forest stands is far greater along the south, east and west than along the north border, and these differences in light significantly affect air temperature, transpiration and assimilation (53*a*).

Light penetration into clear fresh and salt water follows very definite laws. Penetration through turbid water, on the other hand, is more difficult to calculate because turbidity varies so much. Alvik (4) reports absorption of 20% per meter in clear salt water, and absorption of 65% per meter in brown fresh water. Clarke (36) reports that the water south of Bermuda, the clearest sea water known, shows no change in transparency down to a depth

of 133 meters. Measurements by Utterback, Phifer and Robinson (170) in Crater Lake, Oregon, gave light intensities of 11.5 foot candles at 120 meters depth, at a time when the intensity at the surface was 9,000 foot candles. The extinction coefficient for red light was .311 per meter, for green .060 per meter. For blue light there was a change in coefficient with depth from .031, for the first 40 meters, to .035 from the 40th to the 70th meter.

Croxton *et al.* (42) and Egle (49) have measured light transmission through snow. Croxton showed that a negligible amount penetrated eight inches of snow. Egle found transmission through three, five and ten mm. of snow to be 35%, 20% and 5%, respectively. It is obvious, therefore, that plants covered with as much as 20 mm. of snow receive insufficient light for photosynthesis, assuming that temperatures are adequate for this process.

A special case of micro light-climate is that of the exposure of chloroplasts as determined by leaf structure, particularly in thick-leaved succulents. Schanderl (140) and Sauberer (138, 139) have shown that such plants have special means by which the light is transmitted into the leaves to reach the assimilating tissue. These include light-transmitting tannin cells and sclerenchymatous tissue, and orientation of chloroplast along vertical walls, leaving the interior of the cell free to transmit light to inner layers.

Thin-leaved xerophytes and plants of xeromorphic structure that grow on bogs, heaths and other infertile soils, on the other hand, have in their epidermal layer tissue that strongly diffuses the light, thereby protecting the chloroplasts of the palisade against injuriously high intensities (113A).

LIGHT REQUIREMENTS FOR PHOTOSYNTHESIS

Studies of how the photosynthetic process in various green plants is affected by light of various intensities and wave lengths have helped immensely to clarify understanding of the relationship of plants to the light prevailing in their natural habitats. Determinations of quantum relationships between light absorption at different wave lengths and chemical synthesis by the plants indicate that, within the visible region of the spectrum, photosynthesis is almost directly proportional to the amount of energy absorbed by the photosynthetically active pigments (28, 29, 30, 50, 61, 80). This does not necessarily correspond with the total absorption by leaves, inas-

much as inactive pigments and tissues of the leaves absorb energy that can influence photosynthesis only through increasing leaf temperature. Gabrielsen (61) reports that anthocyanin in the epidermis of leaves of *Corylus maxima* var. *purpurea* reduced the photosynthetic efficiency of the light by 43% compared with that of green leaves of *Corylus maxima*. Because of differential reflection and transmission not all wave lengths are absorbed in proportion to their intensity in the incident light. The red region of the spectrum is the most efficient in photosynthesis in proportion to incident energy. Gabrielsen (61) gives values of .38, .60 and 1.00 for relative photosynthetic efficiency in the blue, green and red regions at wave lengths of 440 mμ, 540 mμ and 650 mμ, respectively. Similar values are reported by many other investigators.

The question naturally arises, can an efficient monochromatic light source be found that will produce satisfactory growth of plants? Arthur and Stewart (10) grew buckwheat plants with continuous illumination from several sources, and report their relative efficiency as follows:

incandescent	lamps	1.00
sodium	"	1.41
neon	"	1.20
mercury	"	0.62

It was later discovered, however (9), that certain plants, notably begonia, gardenia, cotton, geranium, buckwheat and snapdragon, tended to degenerate after two or three weeks continuous exposure to sodium vapor lamps, but that this degeneration did not occur if the sodium vapor lamp was supplemented by a mercury vapor lamp. Tomato plants, on the other hand, did poorly when exposed to continuous light from either the sodium or mercury arc or from the two acting together. The hypothesis has been suggested that photosynthesis is more efficient when all regions of the visible spectrum act together than when they act separately. Montfort (107) did not find this to hold for tests on green and brown algae. The concerted opinion of many investigators is that a proper balance of red and blue is necessary for normal development of plants, and that high intensity of a single wave length cannot compensate for inadequate representation of others (40, 44, 136). Johnston (83) states the case well: "Since plants have been growing on the earth for millions of years, it is reasonable to assume that their physiology

is adjusted best to sunlight". Such a conclusion is still a safe working hypothesis for plant ecologists.

Though roughly 50% of solar energy lies within the photosynthetically active region, less than 1% of that reaching the earth's surface at any point is transformed by vegetation into chemical energy in the form of carbohydrates. For instance, the heat value in calories of the wood, bark, branches, twigs and leaves produced annually by an acre of good white pine in Wisconsin is equivalent to only .23% to .5% of the solar energy during the growing season received in an equal area at Madison, Wisconsin (149). Similarly, solar energy utilization by grasses and clover in Bavaria is reported by Noddack and Komor (114) to be .4% to .8%.

But light intensities of 1% or less are far from adequate for maximum photosynthesis. Throughout the range of from 1% to 15% of full sunlight, photosynthesis is almost directly proportional to light intensity, provided other factors essential for rapid photosynthesis are favorable. Should one or more factors be below optimum, photosynthesis reaches a certain plateau value and remains more or less constant with further increase in light intensity. If, on the other hand, all factors are favorable, photosynthesis continues to increase with light intensity until secondary effects set in, such as high respiration caused by high light intensity and high temperature, solarization (the over-accumulation of photosynthate in the leaves and resultant reduction in photosynthesis), water deficit causing closing of stomata, or some other internal limitation. Heinicke and Hoffman (79) found that apple leaves failed to achieve maximum photosynthesis at intensities less than 1,200 foot candles. Carnations require approximately 1,500 foot candles, holly 1,940, radishes approximately 760 (153), dogwood, eastern red oak and white oak 3,000, 3,000 and 1,000 foot candles, respectively, loblolly pine 9,000 (87), *Elodea* 12,000 foot candles (64), *Fucus* two-thirds of full sunlight (81), and tomato plants up to the full daylight intensity at Grand Rapids, Michigan (128).

Solarization and actual injury occur at very high intensity. Myers and Burr (109) demonstrated that *Chlorella* cells were irreparably injured at 40,000 foot candles, and solarization occurred at even lower intensities. Smith (154) published anamorphic curves and derived an equation that expresses the rate of photosynthesis of water plants in relation to light intensity and carbon

dioxide concentrations. This equation gives an exact relationship except for very low rates of photosynthesis.

The ecologist, and particularly the forester, is concerned with what happens when small seedlings growing on the forest floor are suddenly exposed to high light intensity by logging the overstory trees. Harder's (73) extensive studies with water plants bring out one of the principles involved. His plants were cultivated and tested for photosynthetic activity in light intensities having relative values of 1, 4, 64 and 256. Those cultivated in strong light and tested in strong light increased photosynthetic rate with continued exposure to light for a period of some ten hours. Those cultivated in weak light and tested in strong light attained their maximum within one hour, and declined rapidly thereafter. As the light intensity under which they were cultivated increased, the slower were the plants to attain maximum photosynthesis in strong light. Any single species could be made to behave either as a sun plant or as a shade plant, depending upon the conditions under which it was grown.

The slowness of land plants to take advantage of sudden great increases in light is due in part to the differences in structure of leaves developed in shade from those developed in full sunlight. The internal surface of sun leaves may be as high as 20 times their external surface, that of shade leaves nine times their external surface (167). Moreover, the internal surface of sun leaves of xeromorphic structure goes as high as 22 to 31 times external surface, mesomorphic sun leaves, 12 to 16, xeromorphic shade leaves eight to ten. Turrell (168) found that leaves of species that are xeromorphic in high light intensities with respect to the ratio of internal to external area, in low light intensity tend to be mesomorphic.

The tendency of many plants to show a decline in photosynthetic rate at high light intensity serves to minimize the differences in growth rate between shaded and unshaded plants. Stålfelt (160, 161), studying photosynthesis under natural conditions, found that on cloudy days photosynthesis in oats was positively correlated with temperature and light, but on hot bright days the stomata closed and photosynthesis followed the opening of the stomata rather than temperature and light. In high light intensities he found a decline in the rate of photosynthesis in lichen caused by both high temperature and high light intensity. The temperature and light effects

were separable. Tests of photosynthetic rate in intermittent light have shown that when the periods of light and darkness are very short, several alterations per minute, photosynthesis increases markedly with respect to the total amount of light available. This behavior together with that reported by Harder (73) theoretically should enable plants receiving the highly variable light transmitted by the broadleafed forest canopy to grow more rapidly than the average light intensity would indicate. No demonstration has proved this to be true. Nägeli (110) considers sunflecks of negligible importance and diffuse sun and skylight to be chiefly responsible for growth beneath canopies.

The capacity of some plants to achieve a maximum rate of photosynthesis at lower intensities than others may be of some ecological significance. Dogwood, red oak and white oak were found to attain maximum photosynthesis at 3,000, 3,000 and 1,000 foot candles, respectively, whereas loblolly pine increased its photosynthetic rate up to 9,000 foot candles. Kramer and Decker (87) give this as one reason for the ability of hardwoods to invade pine stands, where the maximum light intensity averaged about 4,500 foot candles. Pines, on the other hand, do not invade oak, for there the maximum intensity was only 1,900 foot candles.

Vegetation beneath forest canopies tends to disappear at light intensities below 4% of full sunlight. The density required to exclude herbs beneath deciduous canopies is considerably lower than that required beneath evergreen canopies, probably due to the start such plants can get in the spring before the hardwood leaves are fully developed. The extent to which a forest species can reduce sunlight through the density of its canopy is an indication of its relative capacity to perform photosynthesis at low light intensity. This indication must be used with caution, however, as both conifer and hardwood leaves tend to remain attached on the lower branches even though they consume more photosynthate than they produce.

Just as in forests vegetation tends to disappear at light intensities below 4% of total sunlight, so also water plants tend to disappear or at least to lose their chlorophyll when exposed to intensities of less than 4% (121). Furthermore, when light intensities decline in lakes due to an increase in turbidity, the depth to which plants will grow also declines (120). Manning and Juday (92) found that the chlorophyll content was a fairly good index of the photosynthetic capacity of submerged water plants.

Loose, Pearsall and Willis (90) found that photosynthesis in *Chlorella* occurred down to a depth of eight meters in the Windermere where the light intensity was 5% of full sunlight. The actual compensation point at which photosynthesis balanced respiration was at 2% of full daylight; hence, theoretically the plants could grow at ten meters' depth. But other factors were unfavorable at this depth. No rooted plants grew below 4.3 meters. Extensive studies of photosynthesis in Lake Erie indicated that the compensation point occurred at 2% to 3% of full sunlight (100). This being so, plants should be able to survive down to depths of eight meters, but because of turbidity light intensity is frequently inadequate at these depths. The depths of Wisconsin lakes at which the maximum rate of photosynthesis occurred in *Chlorella* and *Coccomyxa* were found to be five to six meters in a transparent lake and .25 meter in a lake having highly colored water (84). The maximum percentage utilization of solar radiation occurred at ten meters' depth in the very transparent water and at one meter in the highly colored water.

INTERRELATIONSHIP BETWEEN LIGHT AND OTHER FACTORS

Temperature. As less than 1% of the energy which leaves absorb is used in the photosynthetic process, they obviously would soon become overheated were this absorbed heat not dissipated in some manner. The temperature of assimilating leaves under ordinary conditions remains very close to that of the surrounding atmosphere, generally being slightly below air temperature. Temperatures have been reported, however, as much as 7° C. below and 40° C. above air temperature (174). Three methods of heat loss operate to keep leaves very close to air temperature. These are radiation to surrounding objects and to space, convection loss to surrounding air, and heat loss through vaporizing water in transpiration. Curtis (43) believes transpiration to be of minor importance in maintaining leaf temperature, inasmuch as he was unable to demonstrate that high temperatures built up in thin objects that were free to lose heat through radiation and convection. Others have insisted that transpiration plays a dominant role in maintaining leaf temperature (174). It is generally conceded that transpiration may lower leaf temperature 2° to 3° C., or even more (150). As is well known, temperature exerts a major influence

on all biochemical processes in plants. For most there exist minimum, optimum and maximum temperatures. Ashby and Oxley (11) carried out an extensive experiment on the relationship of light intensity and temperature to the assimilation rate and multiplication of fronds in *Lemna*. Sixteen combinations of light intensity and temperature could be studied on 16 separate colonies simultaneously. Experiments were performed at 10°, 18°, 21°, 24° and 29° C., and at light intensities of 80, 150, 350, 500, 750, 900, 1,100 and 1,600 foot candles of light. This gave a total of 40 different combinations of light intensity and temperature. Each experiment lasted from 17 to 20 days. These extensive data enabled them to work out equations showing the relationship between frond multiplication and light intensity. Frond multiplication rate was almost directly proportional to light intensity except at the two lowest intensities. It tended to increase at any specific temperature with an increase of light intensity, and this was more pronounced at high temperatures than at low temperatures. Assimilation rate increased with temperature, from 10° to 29° C., provided only that the light intensity was adequate. The increase was insignificant at 80 and 150 foot candles. From these data they were able to construct three-dimensional models showing the combined effects of light and temperature on the rate of multiplication and net assimilation rate of the fronds.

Ahmad (1), working with *Azolla,* obtained comparable results. For a series of temperatures varying from 7° to 36° C., the growth of *Azolla* increased with increasing light intensity from 35 to 191 foot candles. For each light intensity, growth increased with temperature up to 20° C. and declined at higher temperatures. He presumed that the decrease in growth at higher temperatures was due to increasing respiration, rather than a decrease in photosynthesis. The point at which respiration overbalanced photosynthesis occurred at about 25° under illumination of 35 foot candles, at 35° for 72 foot candles, and was not attained at all for the two higher light intensities, though the values were approaching the compensation point at 36° C.

In contrast to the foregoing experiments in which a single measurement of growth or photosynthesis was made after a definite period of time, are those of Stålfelt (160, 161) involving a series of determinations at short time intervals on the rate of photosyn-

thesis at specific temperatures and light intensities. Both high temperature and high light intensity would produce in *Usnea dasypoga* a relatively high rate of photosynthesis following the initial exposure, but this gradually declined with continued exposure. The optimum temperature for photosynthesis therefore was dependent upon the duration of exposure, and gradually receded with lengthened exposures until the temperature reached 21° C., which proved to be a true optimum for prolonged exposure. Inasmuch as respiration is increased by temperature, the optimum value for apparent assimilation is the result of the action of the inhibiting effect of temperature on photosynthesis and its stimulating effect on respiration. Light acted similarly on photosynthesis. The stronger the light, the quicker the inhibiting effect becomes evident, and the longer light acts the more the rate of assimilation is decreased. Light has a marked influence in increasing the rate of respiration of both green and etiolated tissue (177).

Mineral nutrition. Light, through its effect on transpiration, influences the uptake of mineral salts, and, through its effect on photosynthesis, influences the use of these salts in general metabolism and in the formation of plant tissue. Sun leaves are greater than shade leaves in both fresh and dry weight and in ash (24). Calcium tends to accumulate in proportion to amount of transpiration but potassium does not. Light also increases ash accumulation of plants independent of transpiration, potassium in this instance being affected more than calcium. McCool (98) reports that the injurious effects of manganese on soy beans, snap beans and tobacco could be mitigated by shading, an indication that less manganese was taken up in the shade than in full sunlight. Broyer and Hoagland (25) noted that roots low in salt content and high in sugar have a high potential for salt absorption and in such condition absorb salt at approximately the same rate, irrespective of light intensity and transpiration. But when they have a high salt and low sugar content, salt absorption is more closely related to transpiration. They concluded that transpiration affects but does not govern salt movement.

Low light intensity causes starvation resulting from inadequate supply of the products of photosynthesis. This induces other nutritional disturbances including unbalanced utilization of essential mineral elements. Fred, Wilson and Wyss (59) reported

that soy beans growing in a soil poor in nitrogen but inoculated with root nodule-forming bacteria appeared to suffer from nitrogen hunger if the light intensity was high. This condition could be relieved either by lowering the light intensity or by applying nitrogen to the soil. Best results were obtained by keeping the light intensity constant and applying nitrogen to the soil, but by shading the plants for twelve days and then returning them to the sun good growth and nitrogen fixation occurred. Once a plant got a good start and adequate root nodules were formed, they were able to grow at a satisfactory rate in full sunlight. Gast's (63) very extensive study of the effect of nitrogen and light intensity on the growth of pine seedlings enabled him to develop three-dimensional models showing the relationship between these respective growth factors. If plants are starved for nitrogen they are unable to make adequate use of high light intensity, and, on the other hand, if they are cultivated in low light intensities they are unable to respond by increased growth to a more generous nitrogen supply. Where nitrogen supply was adequate, growth continued to increase up to the full intensity of sunlight. Mitchell (103) found that the total nitrogen content of seedlings cultivated under different degrees of shade tended to increase almost directly with increasing dry weight. Phosphorus content also increased with dry weight, but not to the same extent, whereas total potassium content tended to remain constant, irrespective of light intensity. Or, expressed as percentages of dry weight, potassium and phosphorus decreased with increasing light intensity, but nitrogen tended to remain more or less constant.

Extensive studies of the interaction of factors in the growth of *Lemna* reveal that the optimum nitrate concentration in the growth medium increases with increasing light intensity (180, 181, 182). At the highest light intensities, a decrease in nitrogen supply resulted in an increase in frond numbers but low net assimilation rate, smaller frond area, less protein content and loss of chlorophyll. At the lowest light intensities a decreasing nitrogen supply also increased frond numbers but in marked contrast to the behavior at high intensity, caused an increase in net assimilation, larger frond area, greater protein content, and deeper frond color. This, of course, was simply a reaction to oversupply of nitrogen at the lower light intensities. Both of these factors influenced the basic metab-

olism of *Lemna.* Plants starved for nitrogen had a lower respiration rate than those adequately supplied with nitrogen. The respiration rate also decreased regularly with decreasing light intensity from 1,200 to 900, 600 and 300 foot candles. The decrease in respiration of plants grown in low light intensities is presumed to be due to a decrease in carbohydrate level. In other words, it is a starvation effect. In nitrogen-starved fronds, respiration is affected by two opposing tendencies, that of low nitrogen supply to depress respiration, and that of high carbohydrate concentration to accelerate respiration. The curve of respiration of colonies with full nutrient supply under different light intensities was the same as that for nitrogen-starved colonies, and both were similar to that for real assimilation. Similar disturbances in metabolism and nutrient balance occur in other plants.

Borden (23) found that sugar yields from Hawaiian cane were adversely affected if sunlight conditions were such as to limit the complete assimilation of the applied nitrogen and potassium fertilizers. Nitrogen seemed to be mainly responsible for the decreased sugar yield, but at the same time there must be a proper balance between nitrogen and potassium to obtain cane with the best quality juice. Both nitrogen and sunlight must be adequate for good growth (22).

Blackman and Templeman (21) report that leaf production by *Agrostis tenuis* and *Festuca rubra* subjected to frequent defoliation was markedly increased by applications of ammonium sulphate or calcium nitrate, provided the plants were exposed to full daylight, but if they were shaded these same fertilizing treatments depressed leaf production. Light intensity in this instance greatly altered the ratio of organic acid to carbohydrates. This study confirmed earlier work by the same authors (20) that generous applications of ammonium sulphate and calcium nitrate depressed leaf production of frequently defoliated grasses in 37% and 63% daylight. The lower light intensity interfered with the elaboration of protein, and nitrate tended to accumulate in the plant tissue. The gains in protein as a result of fertilizing in full daylight resulted in a decrease in percentage of carbohydrate content, but at the lowest light intensities little effect on carbohydrate level was brought about by fertilizing. These writers ascribe the effects of light intensity and nitrogen supply on leaf metabolism and leaf production in part to

their indirect effects on root metabolism. The shaded plants, as is well known, tend to use more of their organic food substances to produce leaf and stem tissue than root tissue.

Quite a different effect is that reported by Heinicke (77) on prolonging leaf functioning through autumn application of nitrogenous fertilizer to apple trees, thereby preventing yellowing and early abscission of leaves. With such treatment the foliage remained dark green and stayed on the twigs until temperatures dropped well below freezing. Photosynthesis in excess of respiration continued up to early November. In contrast, the yellowish leaves of the unfertilized trees showed a marked decline in rate of photosynthesis which after October 22 fell below the rate required to balance respiration. Twigs from trees that were fertilized in late fall also proved more winter hardy than those from the unfertilized trees.

Water relations. It has long been recognized that transpiration is affected very strongly by light intensity. Martin (93), in a careful study with sunflower plants exposed to 6%, 19%, 40%, 67%, 70% and 100% solar radiation at noon, found transpiration to be a linear function of radiation intensity. The slope of the line was inversely proportional to the age. The intercept on the transpiration axis and the fraction of transpiration, 38% to 81%, due to the direct effect of radiation, both depended upon the evaporating power of the air.

A very excellent study of the combined effects of varying light intensities and soil moistures was made by Clements and Long (37). Sunflower plants were grown under shades transmitting 11%, 19%, 27%, 44%, 65% and 100% light intensities, and in soil moistures of 14%, 18%, 26% and 35%. At each soil moisture, growth in terms of dry weight increased with increasing light intensity up to full sunlight, with the single exception of 14% moisture. And for each light intensity the growth increased with soil moisture up to the highest value used. The water requirement, that is, the water evaporated per gram of dry weight, was greatest in 11% light and 35% soil moisture. It was least at 100% light and 14% soil moisture. This very significant study has important implications in considering the relative importance of various factors in the growth of plants under natural conditions. Plants grown in high light intensities have long been known to have

higher percentage dry matter than those in low intensity (89). Heinicke and Childers (78), studying apple leaves, found that the rate of photosynthesis gradually declined as the moisture content of the soil decreased. They also found, however, that the early closing of stomata associated with reduced water supply tended to conserve water to a greater extent than it reduced photosynthesis.

Extensive studies by Schneider and Childers (142) show that photosynthesis of apple leaves is very closely correlated with transpiration. As the soil gradually dried out there was, first, a reduction in rate of transpiration, and one day or more later, a reduction in photosynthesis. A marked reduction in both photosynthesis and transpiration and an increase in respiration took place before wilting was evident. Fairly high rates of photosynthesis were obtained on several occasions when the stomata appeared to be closed.

Growth, form, and substance. Growth is the net result of the combined action of all growth factors. As the preceding discussion has brought out, maximum growth is dependent upon a favorable combination of all. When all other factors are present at appropriate levels, many temperate zone plants, particularly woody plants with thick crowns, are able to increase their growth rate with increasing light up to the full intensity of natural sunlight (68, 99, 106, 152). With such plants some of the leaves at any one time may be receiving more light than they require and others less; also, within individual leaves, some of the chloroplasts may be receiving more light than they require and others less. It is the combined functioning of all the chloroplasts in all leaves throughout the day and growing period that determines total photosynthesis and, in consequence, the growth rate.

Thut and Loomis (163) studied the effect of light and temperature on stem elongation of asparagus, field bindweed, castor bean, and on leaf elongation of maize. When soil moisture was adequate and relative humidity high, growth followed the temperature curve very closely. When moisture supply was inadequate either because of low humidity or low soil moisture, growth was checked during midday. These workers conclude that the four plants tested are never inhibited in growth rate by the action of light directly. Indirectly, light increases growth by increasing the rate of photosynthesis and by increasing temperature.

Benedict (18) cultivated three species of range grass in 28%, 45%, 57% and 100% light from June 7 to October 1, at Cheyenne, Wyoming, where, due to high elevation and infrequence of cloudy weather, the total light received is high. All degrees of shading caused increases in height but decreases in dry weight. McCalla and his co-workers (97) attempted to determine by multiple correlation analysis the relationship of growth to light and temperature for maize and gladiolus. They report that growth was directly correlated with temperature and inversely correlated with light. No measurements of light intensity were taken. Growth was measured at four-hour intervals throughout the course of the day and night. They noted a tendency of light to depress growth during midday, very likely due to a water deficit. The actual growth, however, frequently was just as great during midday as at any other time because then the temperature was most favorable.

Gast (63), in careful work with pine seedlings in nutrient cultures, found that the dry weight produced during a growing season could be expressed by the equation,

$Y = A \log R + B$ where
Y = dry weight in grams
A = a constant determined by species
R = cumulative solar radiation in gram calories per square centimeter
B = a constant dependent on species and initial seed weight

The validity of this relationship was further confirmed by Mitchell and Rosendahl (106).

Because few plant habitats present optimum conditions of growth factors other than light intensity, some degree of shade is not always harmful and frequently proves beneficial. Neel (112) found that the yield of a pasture in terms of days animals could be grazed and the total gain in weight of the animals was not reduced significantly by the shade of locust or walnut trees up to an age of 13 years. The shade, however, was kept moderate by pruning the trees. The percentage of blue grass tended to increase as the shade developed. Two important tropical crops, coffee and cacao, do not thrive well without shade. Normally, this is provided by growing them beneath the shade of such light-foliaged trees as *Inga* and *Erythrina*. Arrilaga and Gomez (7) found that Arabian coffee grown under lath shade in Puerto Rico did best with one-third sunlight, but that yield was approximately equal with one-third and one-half sunlight. With two-thirds light, the trees were sickly and the

yield low. Cobley (38) cultivated cacao in one-fourth, one-half, two-thirds and full sunlight in Trinidad. Optimum growth occurred in one-fourth sunlight. This was many times greater than growth in full sunlight.

Very intense light, especially that containing a strong component of ultraviolet, tends to destroy chlorophyll and may lead to the death of plants. Light tends to stimulate respiration both of green and of colorless tissue (57, 65, 130*a*). The ability of different species of plants to develop protective devices against too intense light varies greatly, and to this variation Collaer (39) has ascribed the ability of *Pinus cembra* to survive at higher elevations than *Picea excelsa*. Such devices include all sorts of mechanical means of protection against water loss and against excessive absorption of radiation, such as waxy bloom, hairiness, thickness of leaves, orientation of leaves towards the light, and light-diffusing tissue (123, 113*a*). They also include changes in pigment concentration, chloroplast arrangement and the presence of protective pigments (61). The water plant *Potamageton,* for instance, has both floating and submerged leaves. The floating leaves have a strong red color due to the presence of carotin granules, whereas the submerged leaves of the same plants are green in color. Arens (6) has found that if the red floating leaves are submersed or cultivated in reduced light intensity, they turn green, whereas the green submersed leaves, if placed on the surface or cultivated in high light intensity, turn red.

Langham (88) has found that prostrate forms of several grasses, together with corn and rice, are negatively phototropic under high light intensities and positively phototropic when shaded by burlap. All tended to grow erect in darkness. Leaves show remarkable increases in thickness, intercellular space, size of cells and stomata, and layers of assimilating tissue in high light intensities (82).

Of particular importance is the effect of light on root development and shoot-root ratios. Blackman and Templeman (21) present evidence that nitrogen supply and light intensity markedly affect the leaf-root ratio, and that at low light intensity leaf production takes place at the expense of roots. The rooting of slash pine was found by Mitchell (104) to be favored by high light intensity, high humidity, and temperatures of 65° to 75° C. The light intensity in this case undoubtedly acted through its influence on the

available photosynthetic food supply. Length of *Lemna* roots was found by White (181) to be directly related to light intensity over a range of 50 to 300 foot candles, irrespective of the level of potassium supply. Reduction in either light or potassium supply at all levels, however, did tend to decrease root length, but with potassium this appeared to be an indirect effect caused by a decrease in the net assimilation rate.

Light has other important effects on the development of plants. Those kept in darkness remain colorless, fail to unfold leaves and have excessively elongated stems. Both blue and red light are effective in preventing etiolation, their effectiveness increasing with intensity (56). Infrared, on the other hand, stimulates elongation. Platt (125) has found that the tendency of certain wheat varieties to develop solid stems is favored by high light intensity. Apaoan (5) reports that shading reduced the growth of tillers and delayed the development of rice plants. It also resulted in poor seed. Plants fail to flower under temperature and day length conditions normally adequate for flowering, if the light intensity happens to be too low. *Chrysanthemum* and *Euphorbia,* for instance, failed to flower when the maximum intensity of light to which they were exposed had been reduced to 500 foot candles by cheesecloth shade (129). Light appears to influence the proportion of cleistogamous flowers produced by various plants. Trent (166) reports that in 50% light intensity *Specularia perfoliata* produced cleistogamous flowers but no open flowers; in full sunlight it produced both types.

Chlorophyll, the carotinoids, the anthocyanins and various other pigments and substances that play an active or protective role in the life of the plants are profoundly influenced by light (3, 115). Of great importance to animals is the influence of light on the formation and accumulation of various vitamins in plant tissue, particularly vitamin D and ascorbic acid (70, 132, 133, 134, 135, 137). Shaded potato plants produced tubers low in specific gravity, dry weight and mealiness, and if grown with a high nitrogen supply, incidence of blackening in the tubers was increased (111). Arrilaga and Villamie (8) report that oil in lemon grass is produced in the highest amount and highest quality by the full intensity of tropical sunlight.

Plants inadequately nourished because of low light intensity tend to be more susceptible to noxious gases such as SO_2 (145) and to

infection by plant diseases (75, 76). Cotton bolls tend to shed if kept for as long as three days in darkness or under illumination of 50 foot candles (48). Shading was found to be particularly harmful after flowering.

LIGHT AND SUCCESSION

Light intensity is only one of several factors influencing plant succession. It probably becomes dominant only after succession has advanced to such a stage that the plant cover is sufficient to reduce light intensity to below 20% of full sunlight. Inadequate nutrient and moisture supply and inadequate protection against moisture loss, extremes of temperature, unstable soil and wind action may prevent plants from colonizing open areas. Yet when these same areas are given some protection by shading, vegetation may become established and thrive (117). Such stages of succession are clearly governed by factors other than light intensity. Certain herbs and field crops, notably red clover, are capable of growing so rankly that they shade out white clover or other low-growing plants, but ordinarily it is not until the advent of woody plants, both erect and climbing forms, that shade begins to play an important role in succession. Pioneer woody species such as gray birch, eastern red cedar, the Rocky Mountain junipers and pinon pine rarely cast a dense enough shade to preclude invasion by other species. Their shade and root competition may, however, markedly reduce the growth of invaders, but as the pioneers drop out seedlings of longer-lived species take over. So succession proceeds from the thin-foliaged scattered stands to the thick-foliaged dense stands. And as it proceeds, competition for light becomes more and more keen. Under these conditions the plants that actually attain a foothold beneath forest canopies are those species whose seeds are able to germinate and whose seedlings are able to persist for long periods in light of low intensity. Seedlings of such species —usually already established on the forest floor—are the ones that as a rule pre-empt the space left by the death of veterans and ultimately form the climax. But when timber cutting, windstorm, insects or disease open up large areas of forest, these advance seedlings, suddenly exposed to full sunlight, may succumb because of unbalanced root development and tender leaves.

Ståfelt (159) has shown that branches and twigs of Norway

spruce that had been subjected to shade for a considerable period of time reacted in three ways to thinning. Branches that had been heavily shaded died when exposed to intense light; those formerly receiving abundant light opened normal buds and developed adventitious buds which, without thinning, would have remained dormant. On the other hand, branches which had been growing in weaker but still favorable light before thinning continued growth, but with development of heavier foliage. The old shade needles frequently dropped off completely and the new ones developed after the thinning showed an increase in diffusion capacity.

Closely related to natural succession are the successions artificially induced when foresters plant trees on lands occupied by other plant associations. Filzer (54) studied the behavior of the Scotch broom association in the Swabian Alps as modified by planted pines. The pines did not cause complete elimination from the area of plants characteristic of the Scotch broom association. Only those unable to endure the shade of the pines died. The same sort of selective succession occurred also where pines were planted on land formerly dominated by heather. The associations brought about by planting, therefore, were heterogeneous containing, in addition to the planted trees, those elements of the original association that could withstand the shade, plus new species capable of invading the pine community but unable to invade the original association.

The controversy over which is the more important, light or root competition, in determining seedling establishment and the course of natural succession beneath forest canopies is still a live one. But work during the past ten years goes far to clear up misunderstandings. The controversy has pivoted around whether the concept of tolerance as used in forest and ecologic literature should be defined as the capacity to endure shade, or the capacity to endure all factors of competition including root competition for moisture and nutrients (85, 164). In recent discussions of this question, Shirley (151, 152) points out that the relative capacity of jack pine, red pine, white pine and white spruce to endure shade in the Lake States increases in the order named and that natural succession proceeds in this order. Their relative juvenile growth rates and vigor, irrespective of light intensity and resistance to drought, in soils deficient in nitrogen and phosphorus, are in the

exact opposite order. Resistance to heat injuries and recovery therefrom, and establishment, survival and root penetration of first year seedlings are species characteristics which are independent of light, moisture and nutrient requirements.

Harley (74) reports that European beeches grown under artificial shades transmitting 10% light resembled those grown in natural woodland shade in having relatively high water content, poor root growth, low dry weight of both root and shoot, low ratios of root to shoot, incomplete mobilization of nitrogen before the fall of the cotyledons, and a very low rate of nitrogen absorption. Harley concluded: "These experiments therefore indicate definitely the immense importance of light intensity under woodland conditions, and also show that the complications arising out of soil composition and structure are of secondary importance at the early stage of the life of the beech".

Shirley (152) reports on extensive experiments in which both light intensity and root competition were varied. At each light intensity growth could be increased by decreasing root competition, and at each level of root competition growth could be increased by increasing light. However, the increase in growth rate never was as great where only one factor was improved as where both were improved.

Low light intensity, through stimulating top growth at the expense of root growth, tends to increase susceptibility to summer drought in regions of deficient rainfall (19, 69). The preponderance of evidence seems to be that the requirements of the several species for moisture, nitrogen, light and other growth factors need not be confounded (66, 105, 117, 118, 122). Precision demands that their effects be considered individually and in relation to one another and not as a single, complex, inexplicable entity.

There is an effect of root competition quite aside from that due to competition for moisture and nutrient supply that merits consideration. This is the so-called "root antagonism"—the inability of one plant to thrive when its roots grow in soil permeated by the roots of certain other plants. Interest in this subject, long dormant after it was first discovered, has been revived by agronomists because of its importance in pasture grass management. Schreiner (143, 144) has found that sod inhibits growth of hybrid poplars planted in fertile, well-watered soils. He has also discovered that

the effect could be produced by growing poplars in nutrient solutions that first had passed through cultures in which grasses were growing, even though the solutions were renewed before showing detectable depletion of nutrient elements. Coster (41) reports that a rich and varied undergrowth occurred beneath a dense canopy of *Lagerstroemia stegoisa* and *Ficus kurgii,* whereas no undergrowth occurred beneath a canopy of *Swietenia macrophylla* transmitting two to three times as much light. Coster attributes the difference to shortage of water caused by the strong root competition of mahogany, but root antagonism also may have been a factor.

This further emphasizes the desirability of seeking through factorial design of experiments and multiple correlation analysis, to work out the true interrelationship of the several growth factors of plant habitats. To confound them with one another inevitably confuses thinking, thereby adding mystery to subjects open to clear analysis. Succession can best be understood by accurately appraising the several growth factors of the habitat and understanding the respective requirements of the several species involved for light, moisture, heat, nutrients and other survival and growth elements.

As, more and more, man seeks to use the vegetation of deserts, fields, grasslands and forests for economic ends, the more important it becomes that he understand the action and interaction of the several growth factors in determining the composition, growth, vigor and perpetuation of plant communities. Rapid strides have characterized research of the past ten years. The coming decade should see this and new work integrated into handbooks and guides for the successful management of natural vegetation. Only then does the information become available to the practitioner and thereby serve its fullest usefulness. And only then can the research worker quickly appraise the status of information on a specific type or association and thereby direct his research work to those subjects most in need of further study. Precise ecologic information grows in importance and usefulness yearly. Its diligent search and collation is a worthy scientific and public service.

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Antibiotic Substances Produced by Fungi	D. F. HOLTMAN *University of Tennessee*
American Agar Industry	H. J. HUMM *Duke Marine Laboratory*
Destructive Foreign Plant Diseases not known to be established in North America	N. REX HUNT *Bureau of Entomology and Plant Quarantine*
Cell Walls	T. KERR *North Carolina State College*
Techniques for Aseptic Growth of Plants	L. C. KNORR *Cornell University*
Protoplasmic Connections	L. G. LIVINGSTON *Harvard University*
Endomitosis	A. LORZ *Seton Hall College*
Tropical Fruits and Their Future	S. J. LYNCH *Sub-tropical Experiment Station*
Paleobotanical Taxonomy	H. L. MASON *University of California*
Cell-shape	E. B. MATZKE *Columbia University*
Recent Advances in the Science and Technique of Seed Analysis	R. H. PORTER *Iowa State College*
Polyploidy	L. F. RANDOLPH *Cornell University*
Distribution and Composition of Paleozoic Floras in North America	C. R. READ *U. S. Geological Survey*
Phylogeny of the Basidiomycetes	D. P. ROGERS *Brown University*
Cell Physiology	G. W. SCARTH *McGill University*
Botanical Contributions to the Study of Coal	J. M. SCHÖPF *Illinois State Geological Survey*
Recent Developments of Taxonomic Agaricology	A. H. SMITH *University of Michigan*
History of Arctic and Alpine Floras	C. W. SHARSMITH *University of Minnesota*
Phytogeography of the Temperate West Coast of South America	H. E. STORK *Carleton College* and J. L. MORRISON *University of California*
Environment and the Cereal Smuts	V. F. TAPKE *U. S. Bureau of Plant Industry*
Nematode Diseases of Plants	A. L. TAYLOR *Bureau of Plant Industry*
Taxonomy of North American Fresh-Water Algae	L. H. TIFFANY *Northwestern University*
Measurement of Soil Moisture	F. J. VEIHMEYER *University of California*
Utilization of Native Plants by the American Indians	P. A. VESTAL *Harvard University*
Vegetable Seed Treatment	J. C. WALKER *University of Wisconsin*
Modern Views and Facts About Growth Substances	P. W. ZIMMERMAN *Boyce Thompson Institute for Plant Research*

Proposed Future Contents of
THE BOTANICAL REVIEW

Articles received and awaiting publication

Cytotaxonomy of Nicotiana	T. H. GOODSPEED *University of California*
Tissue Responses to Physiologically Active Substances	BETTY F. THOMSON *Connecticut College*
Bacterial Galls	A. J. RIKER *University of Wisconsin*
Detached Leaf Culture	C. E. YARWOOD *University of California*
Root Diseases of Deciduous Fruit Trees	J. S. COOLEY *U. S. Department of Agriculture*
Specialization, Hybridization and Mutation in the Cereal Rusts	T. JOHNSON and MARGARET NEWTON *Dominion Laboratory of Plant Pathology*
Preventing Plant Disease Introduction	W. A. MCCUBBIN *U. S. Bureau of Entomology and Plant Quarantine*
Aerobiology in Relation to Plant Disease	E. C. STAKMAN and CLYDE M. CHRISTENSEN *University of Minnesota*
Cytology and Genetics of Forage Grasses	W. M. MYERS *U. S. Bureau of Plant Industry*
Anthocyanin Pigments of Plants	F. BLANK *Swiss Federal Institute of Technology*
Fatuoid, Speltoid and Related Mutations of Oats and Wheat	C LEONARD HUSKINS *McGill University*
The Effect of Mineral Supply on the Mineral Concentration and Nutritional Quality of Plants	K. C. BEESON *U. S. Department of Agriculture*
Osmosis and the Movement of Water in Plants	T. C. BROYER *University of California*
Physiology of Citrus Fruits in Storage	E. V. MILLER *U. S. Bureau of Plant Industry*

Articles arranged for most recently

A Comparison of the Marine Algae of the Atlantic and Pacific Coasts of North America	G. J. HOLLENBERG *University of Redlands*
Soil Treatment to Eliminate Pathogenic Fungi	F. L. HOWARD *Rhode Island Agricultural Experiment Station*

Articles in course of preparation

The Cytology of Fertilization in Angiosperms	L. E. ANDERSON *Duke University*
Development of the Madro-Tertiary Flora	D. I. AXELROD *University of California*
Rubber Formation in Plants	JAMES BONNER and A. W. GALSTON *California Institute of Technology*
Role of the Endosperm in Seed Development	R. A. BRINK and D. C. COOPER *University of Wisconsin*
Ecology of Marine Algae	V. J. CHAPMAN *Cambridge University*
Heart Rots in Living Trees	R. W. DAVIDSON *U. S. Bureau of Plant Industry*
The Angiosperm Embryo Sac	EMMA L. FISK *University of Wisconsin*

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